COMPARATIVE POSTEMBRYONIC DEVELOPMENT OF ARACHNIDS

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A common model is used to describe the growth of various arachnid groups. In these predators there is retardation of development of the first instars, along with greater maternal care for the clutch and even, as far as some groups are concerned, in a viviparous development. Mites, which have very diversified biologies, have developments which have evolved in many different ways.

Les développements des différents groupes d'arachnides sont décrits en suivant une trame commune. Il apparaît ainsi une évolution des groupes de prédateurs qui se traduit par une augmentation du retard de développement des premiers stades, en liaison avec des soins à la ponte croissants, avec même pour certains groupes des développements vivipares. Les Acariens, de biologies très diverses, ont en conséquence des développements qui ont évolué dans des voies très différentes.□*Development, arachnids, growth.*

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Analysis of developmental types used in arachnids is very great diverse in the terms used to describe these phenomena. This diversity tends to partially hide some similar points in the developmental process. Authors often use terminology and analyse specific to a single group or species, instead of referring to general concepts relating to all arthropods.

This study compares the developmental processes using the same terms, and we will only use specialised terms if it is absolutely necessary. All developments cannot be discussed in detail here; definitions and more precise descriptions can be found in Canard and Stockmann (1992).

METHODS

Our study is based mainly on literature, enriched with our observations on arachnid growth, particularly on spiders and scorpions.

First, we will evoke the main concepts and definitions used and will then define the different scales of development for each taxon. Taxa which are exclusively predatory are here represented by to the increasing level of care devoted to the clutch. Mites, which have diverse biologies, will be studied separately later.

RESULTS

Concepts and Definitions

POSTEMBRYONIC DEVELOPMENT, HATCHING AND BIRTH

The development, defined as initially embryonic, starts with the first divisions of the egg and continues with the formation of tissues. After hatching or birth, the development is qualified as postembryonic. The postembryonic organism is then covered with an external integument and develops outside of the egg membrane or the female's genital tract. Various organs appear and develop, some will not be functional until late developmental stages (e.g. genital organs). Externally, the development is shown by changes in the cuticle. Reiteration of this concept may seem pointless, but the study of arachnids requires some explanations about hatching and birth.

Hatching, i.e. the opening and release from the egg's membrane, can be a long process. It may take a few days for some spiders, and sometimes some moults can be observed between the beginning of the opening of the egg's membranes and their complete liberation. Hence, the postembryonic period does start with the opening of the egg's membranes. This does not make it necessary to look for a phenomenon before hatching as, for example, Legendre (1958) and Vachon (1958b) did as they chose the 'inversion' to define the beginning of the postembryonic period. Moreover, this proposition has one drawback: it makes the postembryonic development begin at a time when the organism is not covered by a tegument.

Birth appears as a well and easily defined phenomenon, without ambiguity. However, in pseudoscorpions, the organism leaves the female's genital tract and moves into a ventral

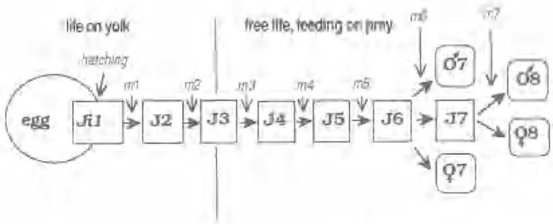

FIG. 1. Stages of postembryonic development of an opilionid, *Liobunum rotundum* (Phalangidae, Palpatores) (after Gueutal, 1943 and Naisse, 1959). (m = moult, **Ji** = incompleted juvenile, J = juvenile).

brood pouch, which is like an external extension of the female's genital tract. Once in the pouch, development continues and the organism still receives nutritive fluid from the mother. Therefore, the start of the postembryonic development of pseudoscorpions should be when they leave the pouch, rather than when they leave the female's genital tract, as others have stated.

INSTARS AND STASES

The instar is the organism between two moults. Generally, among arthropods, the external form does not significantly change between these two stages, except for the short periods of pre- and post-exuviation. However, among some mites, the external morphology and biology are modified while the cuticle remains. Hence, Henking (1882) distinguished two forms, called instars ('stade'), one active and the other motionless. Although this use of the term 'instar' was followed only by a few authors to describe the development of few mites, another acarologist (Grandjean, 1938), considered that the term was too indefinite and proposed the term 'stase'. The definition of stase changed later, but this term is the basis for an evolutionary concept (Grandjean, 1954; André and Jocqué, 1986; André, 1989).

We use 'instar' here in its usual definition, which means an organism between two moults (for endocrinal considerations, see Canard and Stockmann, 1992). To keep the general definition, we will discuss the concept of stase later. When the animal presents separate biologies linked with two different aspects during the same instar, we call them 'forms' and give them two different names.

SUCCESSION OF INSTARS

We limit our study to a morpho-biological description of the successive instars. These instars can follow each other in phase (Vachon, 1953) in which all instars are of same kind. These different types are defined in Table 1.

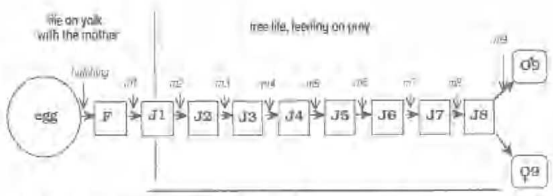

FIG. 2. Postembryonic development scheme of a solpugid, *Eremobates durangonus* (after Muma, 1966).

DIFFERENT DEVELOPMENTAL ROUTES

OPILIONIDS

The eggs are laid isolated from each other and then abandoned. The emergent animal depends on its yolk reserves. It looks like a juvenile harvestman but morphologically differs from following instars by the unpigmented integument and lack of some characteristics, such as unformed chelicerae, unsegmented tarsus, absence of median eyes, etc. Therefore it is an incomplete juvenile: Ji_1 (term taken from Holm, 1940 concerning spiders) (= 'larve' according to Juberthie, 1965). It also has temporary organs (one or two egg teeth located on dorsum of cephalothorax).

After the first moult, the animal differs from the imago only by its size and by sexual characteristics. It is a juvenile, the second of the juvenile phase: J_2 (= 'nymphe' according to Juberthie, 1965). Although active, it still lives on its yolk reserves. After one moult, the juvenile opilionids (J_3) scatter and then feed on prey they catch. Usually, 6-7 juvenile instars occur before it becomes an imago, more rarely there are 5 to 8. The number of moults may vary from with individuals of a species, and according to the developmental conditions; this number is generally the same for both sexes.

On becoming a breeding instar (imagos) the opilionid cease moulting (adults), although some may live for be 5-6 years (Juberthie, 1965).

SOLIFUGIDS

The female isolates herself in burrow but does give care to her eggs.

The animal which hatches is incomplete, motionless and lives on its yolk reserves. It is unpigmented, has no eyes and no racquet organs. Two types may be distinguished. The first is in the Galeodidae (Vachon, 1958a; Junqua, 1966). It does not look like the imago and keeps the aspect it had while under the constraint of the membranes of the egg; it is a foetal instar: **F** (= 'larve' of Vachon, 1958a or Junqua, 1966, = 'post-embryo' of Muma, 1966). The second type is present in some Solpugidae (Lawrence, 1947)

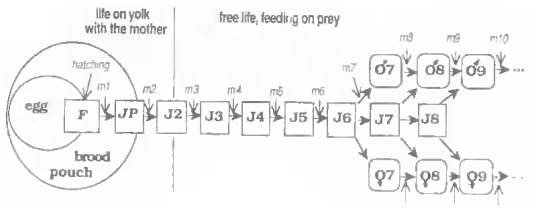

FIG. 3. Scheme of the different stages of the postembryonic development of an amblypygid, *Tarantula marginemaculata* (after Weygoldt, 1970).

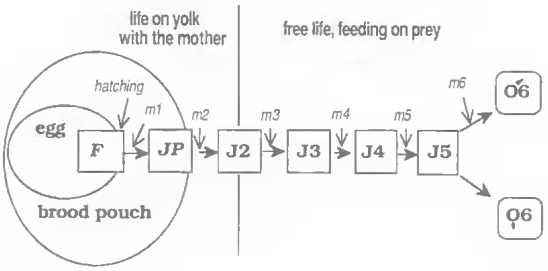

FIG. 4. Scheme of the different stages of the postembryonic development of *Typopeltis stimpsonii* (Thelyphonidae) (after Yoshikura, 1965).

and some Karschiidae (Thaler, 1982). It looks like the imagos (juvenile), but lacks some structures and has temporary organs like thorny continuations of the legs. It is an incomplete juvenile: Ji_1 (= 'primärlarve' of Thaler, 1982).

A further moult results in an animal which has all the adult organs, except those linked with reproduction. This juvenile is, according to the species, the first or the second of the phase (= 'nymphe' of Vachon, 1958a; Junqua, 1966; Muma, 1966). It remains with the female until its integument is hard enough, then it disperses and lives on its own, feeding itself on prey it catches. The number of instars before reaching the status of imago varies according to the individuals. The imagos have a short life expectancy comprising only one instar (adult).

Amblypygids

The female carries the eggs under its abdomen in a brood pouch generated by the genital tract during egg-laying. The incubation period of the clutch may last 3 months (Weygoldt, 1970). Hatching takes place in the brood pouch.

The organism released from the egg's membranes has a foetal aspect with the prosoma bent towards the abdomen and its appendages tight along the body. It is very incomplete (appendages incompletely segmented, absence of setae and of sensory organs, etc.), motionless and lives on its yolk. It is a foetal instar: **F** (= 'deutembryo' of Weygoldt 1970).

After one moult, the animals leave the brood pouch and attach themselves under the females's abdomen. They still live on their yolk, can move, and look like imagos (juvenile), but some structures are lacking and the internal organisation is incomplete (digestive tract, circulatory system, etc.). It is an incomplete juvenile instar which has particular organs on the legs, a dorsal continuation at the distal end of the tibiae (Weygoldt, 1970) and, in some families, an adhesive organ at the tip of the tarsus. It lives on the mother and is adapted to this life, so with reference to Scorpions, we call it the pullus: **JP** (= 'embryon' of Pereyaslawzewa 1901, and 'praenymphe' of Weygoldt 1970).

The pullus moult while on the mother and then leaves her. Through this moult it acquires all the characteristics of the adult (except the reproductive organs). It is a juvenile instar: J_2. After a short gregarious period, the juveniles scatter and live on their own, feeding themselves. The number of juvenile instars may vary between individuals (Weygoldt, 1970) and, after one year, they become an imago.

The imagos of both sexes go on moulting and, under good conditions, the females keep growing after this moult. Therefore, there are no 'adults'.

Uropygids

The female isolates herself in a burrow, and lays her eggs in a newly secreted transparent ventral sac.

Hatching occurs in the brood pouch. It corresponds to a quasi-simultaneous release of the egg's membranes and of the integument of an instar similar to the foetal instar of the Amblypygids: **F** (= 'primärlarve' of Kästner, 1949 and 'prelarva' of Yoshikura, 1965). This instar, which was already formed in the egg, has a very short postembryonic life.

The animal released after hatching and after the first moult, can move and climb upon the mother's back. In general morphology, it looks like the adult (juvenile phase), but lacks some organs (median and lateral eyes are not yet visible, flagellum unsegmented, etc.). It has particular organs linked with its life on the mother, including pad-like organs at the tip of the legs, instead of claws. It is a pullus: **JP** (= 'sekondärlarve' of Kästner, 1949; 'larva' of Yoshikura, 1965). After a 'diapause', there is a moult which releases a juvenile instar: J_2 (=

Forms	Characteristics			Symbols
Non-breeding	different morphology from imagos	motionless instars which do not feed themselves	embryonal aspect unsegmented appendages	foetal instar
			segmented appendages	nymph
		active instar		larva
	same morphology as imagos	several organs which do not function	no temporary organs	incomplete juvenile
			temporary organs linked to life on mother	pullus
		only non-functional genital organs		juvenile
Breeding (= imagos)		with moulting		imago

TABLE 1. Characteristics of different kinds of instars.

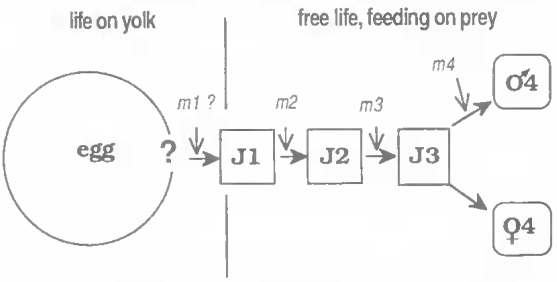

FIG. 5. Scheme of postembryonic development of *Prokoenenia wheeleri* (after Rucker, 1903).

'pullus' of Kästner, 1949; = 'protonymph' of Yoshikura, 1965). They are still gregarious but move around the burrow and begin to feed themselves. After one winter spent together, they then moult and scatter. Subsequent moults usually occur annually, but may be less frequent (Yoshikura, 1965).

Imagos do not seem to moult (adults). Their size of each species does not vary much.

Palpigradids

The sexual biology of palpigradids is almost unknown. Moreover, nobody has ever succeeded in breeding palpigradids. Therefore, knowledge about their postembryonic development is based on observations of natural populations. Under these conditions three immature instars have been determined for many species (Condé, 1984).

The three instars of *Prokoenenia wheeleri* correspond to juvenile instars (Rucker, 1903). Their morphology evolves in a quantitative manner (number of bristles, articulations of the flagellum, evolution of genital parts, etc.).

Spiders

The degree of maternal care given to the clutch varies between species. Some spiders abandon their cocoon (e.g. araneids). Others carry it in their chelicerae or attached to their spinnerets.

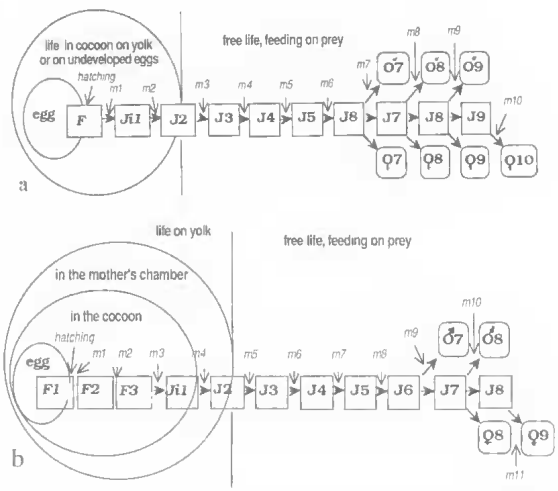

FIG. 6. Postembryonic development in two spider species that (a) abandons its clutch (*Larinioides cornutus*) (after Ysnel, 1992), and (b) cares for young (*Philaeus chrysops*) (after Bonnet, 1933; Canard, 1984).

Others keep their clutch with them in their silk chamber (e.g. salticids).

Hatching occurs in the cocoon and it sometimes takes a few hours before the first instar is released. This instar is generally foetal: **F** (= 'prélarve' of Vachon, 1958b, = 'pullus' of Canard, 1984). Among some orthognathids it remains intrachorional and is therefore not postembryonic. Its very thin cuticle bursts during hatching when the egg membranes open. Among several species which give care to the clutch, there is a series of 2 or 3 instars of this kind: $\mathbf{F}_1$, $\mathbf{F}_2$, $\mathbf{F}_3$ (Canard, 1987). As they cannot move, they stay in the cocoon.

The following instars are mobile and look like a spider (juvenile) but the first one or two still lack some adult characteristics: they are incomplete juvenile (**Ji**) (= 'larves' and 'prénymphes' of Vachon, 1958b). In some cases, the first instar of

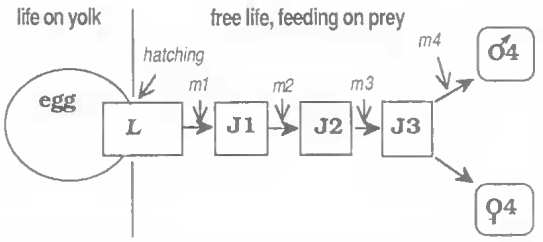

FIG. 7. Scheme of postembryonic development stages of ricinuleid *Crytocellus palaezi* (after Pittard and Mitchell, 1972).

this phase is very incomplete, but in some others, some characters can only be shown absent using an SEM. These first incomplete juvenile instars live on their yolk, but some also feed on undeveloped eggs, which they can pierce with a cheliceral blade. Dispersal takes place after the moult which releases a juvenile equipped with all its organs (**J**). Juveniles then live on prey they catch (= 'nymphes'; Vachon, 1958b). The total number of juvenile instars may vary within a species. Males often become an imago in fewer instars than females.

Female orthognathids and filistatids can still moult. In labidognathids, imagos do not moult any more (adults). In nature, all male spiders die without moulting.

Ricinuleids

Hatching releases an active individual, which catches prey but which has only three pairs of legs and therefore does not present the general arachnid characteristics. It differs from the imago, and is a larva: **L**. The three instars that follow resemble the imago, and possess 4 pairs of legs; however, they lack genitalic structures. They are juveniles instars: $\mathbf{J}_1$, $\mathbf{J}_2$, $\mathbf{J}_3$ (= 'nymphes' of Pittard and Mitchell, 1972). There is only one imaginal instar (adult).

Pseudoscorpions

The eggs are laid in a brood pouch where they feed upon maternal nutrients with the aid of the embryonic membrane. Growth of the embryos bursts the chorion and the external side of the brood pouch to which they remain attached by the buccal region. Their form is not differentiated. Within a few seconds, the mother injects a nutritive fluid which trebles their volume (= 'larves gonflées' of Vachon, 1938; 'deutembryons' of Weygoldt, 1969). Organogenesis continues and a moult occurs which releases an animal which emerges by an anterior cephalothoracic tooth.

The released instar looks like the imago, but

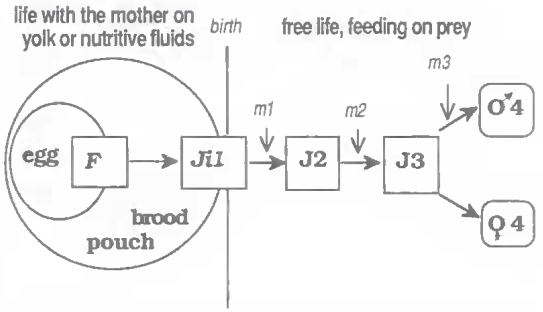

FIG. 8. Postembryonic development of a pseudoscorpion, *Chelifer cancroides* (after Vachon, 1938).

retains some non-evolved characteristics (sensorial system, silk glands, digestive tract, etc.). It is an incomplete juvenile: $\mathbf{Ji}_1$ (= 'larve II' and 'protonymphe' of Vachon, 1938; 'protonymph' of Weygoldt, 1969). Some species apparently retain a foetal aspect (Judson, 1990). The first free instar sometimes remains and moults in the chamber constructed by the female (Weygoldt, 1969). The animal lives alone after this moult. The number of following juvenile instars is fixed to two: $\mathbf{J}_2$ (= 'deutonymphe'), $\mathbf{J}_3$ (= 'tritonymphe'). Each instar can be identified through its trichobothriotaxy (Vachon, 1938). Imagos do not moult any more.

Scorpions

Eggs hatch in the female's genital tract (viviparous species) or soonafter laying (ovoviviparous species).

Newly born scorpions climb onto the mother's back and remain there, living on yolk reserves. They resemble an adult (juvenile) but is incomplete (without trichobothria, unpigmented integument, without specific bristles, etc.). It has temporary organs linked to life on the mother's back, such as legs without claws but bearing adhesive organs at their tip. This incomplete juvenile is a pullus: **JP** (= 'larve' of Vachon, 1940).

After one moult on the mother's back, the juveniles periodically move to the ground, where they begin hunting and eating for the first time. They disperse afterwards and live alone. The second instar is a complete one ($\mathbf{J}_2$). The number of juvenile instars may vary according to sex. Mostly there are 6 to 7 instars, but it may vary from 5 (*Orthochirus*) to 10 (*Diplocentrus*) (Polis, 1990). Imagos do not seem to moult, but it may be possible (Stockmann, 1968).

Mites

The Acari have many more developmental

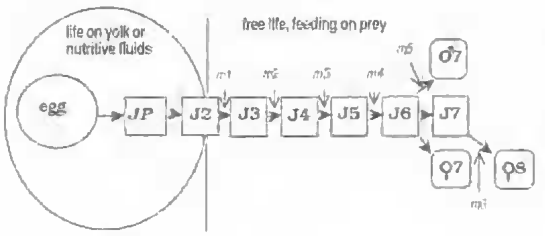

FIG. 9. Postembryonic development stages of a scorpion, *Euscorpius italicus* (after Angermann, 1957).

types than other arachnids. The eggs are often abandoned. There is a first instar which has a foetal aspect, but it remains intrachorionic, except in some cases (Coineau, 1977). This instar can be compared with foetal instars of other arachnids (F), but it is not postembryonic.

The first free instar is obviously different from the imago because it usually has only 3 pairs of legs. It moves and can feed itself. It is a larva: L.

The following instars are eight-legged and only differ from the imagos by some quantitative or sexual characteristics: they are juveniles (J) (= 'nymphes'). The number of instars is often fixed for a species, at 1 or 2, more often a maximum of 3, but up to 4-5 in the Argasidae.

After these immature instars imagos appear, which do not moult anymore (adults) (= 'prosopon' of Reuter, 1909).

In the thrombidiids, there are periods of inactivity between larval and juvenile stages and between juvenile and adult stages. At such times, the animal is covered by the original cuticle, but secretes a new tegument under it, which becomes the tegument of the next instar. In many other cases, motionless instars can be distinguished, sometimes comparable to real nymphs or to specific survival-forms, which allow for dispersal.

DISCUSSION AND CONCLUSIONS

Terminology and Concepts

Most terms used in other arthropods can also be used in arachnids. We have used only the original terms of pullus, foetal instars and incomplete juvenile.

The foetal instar, although it has been defined for arachnids (Canard, 1987), is not specific to this group. It is evident in some insects and myriapods (= 'prolarves', 'prélarves', 'pseudofoetus', etc.).

The incomplete juvenile instars belong to the juvenile phase of which they form a part (J_1 followed by J_2). One can recognize the systematic group of the imago, therefore they are not larvae, but genital organs and furthermore some other structures are lacking. This 'incomplete' situation is not always easy to observe morphologically. However, biological information is useful, because these instars are nearly always unable to live on their own.

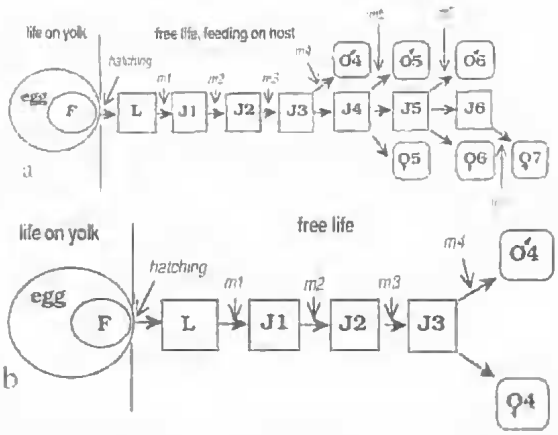

FIG. 10. Succession of stages in postembrional development of mites, (a) Argasidae, *Ornithodoros maritimus* (after Guiguen, 1990); (b) Oribatidae (*Carabodes wilmanni*) (after Bellido, 1983).

The pullus (Pavlovsky, 1924) is an incomplete juvenile instar with special adaptations to life on the mother, such as pad-like organs on the tip of the legs.

The presence of two morpho-biological forms during the same instar among mites is rare amongst the arthropods (except Diptera), but it does not raise any problems of description and does not require any fundamental vocabulary changes; it simply requires more accurate definitions.

Chronological and Morpho-biological Descriptions

In the development of a systematic group of arachnids, except in ricinuleids, pseudoscorpions and perhaps palpigradids, there is no fixed number of instars. Therefore it would be unwise to base a study on few species and to fix the chronology, because some still unknown developments may modify the established system. Theoretical systems of this kind were proposed by Reuter (1909) for mites and by Vachon (1958b) for spiders. Thus, the constant presence of three post-larval juvenile instars (=nymph) in mites stated by Reuter and often followed (protonymphe, deutonymphe, tritonymphe) does not conform to most species,

in which there are less than 3 juvenile instars and even less to those with 4 to 6 instars (e.g. *Ornithodoros maritimus*).

Developmental analyses based on a fixed number of instars (chronological) establishes common points between instars of different species, in order to envisage evolutionary pathways. But these common points will always remain hypothetical, and moreover, these pathways can be elucidated without this system. Therefore we do not wish to use a method with no decisive advantages and, because of its fixed character, limited development descriptions, because species which do not suit the established system are excluded. In mites, for example, the number of instars is considered fixed to one larval, three juvenile instars and the adult. However, in many species one or more juvenile instars are missing and sometimes there are more than three juvenile instars. For mites there is, depending on the species, a variable number of instars.

Evolutionary Pathways

Immature instars of arthropods are adapted to special lifestyles or environments and sometimes differ from those of imagos. Often these adaptations influence the morphology so deeply that it is difficult to distinguish the imago from the immature forms (larva). Such differences are less marked among the arachnids (larvae absent except in mites and ricinuleids).

A good correlate probably exists between the increased level of care by the mother to its clutch and the increased number of incomplete instars at the start of the development.

Moreover, the biology and morphology of early instars can be observed and explained as adaptations to life in the cocoon or with the mother, e.g., the temporary organs such as distal, pedal pad-like organs of pullus (attaching to the mother) or the cheliceral blade of some incomplete juvenile spiders (feeding on undeveloped eggs). The viviparous cases do depend on the same kind of evolutionary processes.

The evolution of many arachnids has probably been characterized by growing care of the clutch correlated with the increasingly and later development of the first instars. Thus, the instars are both incomplete and regressed, because these adjectives depend on the point of view considered: ontogenetic or evolutionary. This corresponds to the 'deux temps' of Grandjean (1954) and, to a certain extent, to the 'state approach' and the 'stase approach' of André (1989).

Mites present great diversity in their biology and, unlike other arachnids, are not all predators. Therefore, they have followed different evolutionary pathways and sometimes metamorphosis takes place, with larvae and nymphs (similar in these cases to those of holometabolic insects) or with 'survival' instars which enable them to disperse.

This evolution of clutch or juvenile care by the mother does not indicate phylogenetic relations in the different orders, because it is a general phenomenon within the animal world and can appear independently in different groups.

LITERATURE CITED

ANDRÉ, H.M. 1989. The concept of stase. Pp. 3-14. In: H.M. André and J.C. Lions (eds). 'L'ontogénèse et le Concept de Stase chez les Arthropodes'. AGAR: Wavre.

ANDRÉ, H.M. & JOCQUÉ, R. 1986. The definition of stases in spiders and other arachnids. Mémoires de la Société Royale Belge d'Entomologie 33: 1-14.

ANGERMANN, H. 1957. Uber verhalten, Spermophorenbildung und Sinnesphysiologie von *Euscorpius italicus* Hbst. und Verwandten Arten (Scorpiones, Chactidae). Zeitschrift für Tierpsychologie 14: 276-302.

BELLIDO, A. 1983. Etude morphologique et écologique de *Carabodes willmanni* Bernini, 1975 (Acari, Oribatei) dans une formation pionnière de la lande armoricaine. Thèse 3ème cycle Rennes I. 79 pp.

BONNET, P. 1933. Le cycle vital de *Philaeus chrysops* Poda (Aranéide, Salticide). Archives de Zoologie Expérimentale 75: 129-144.

CANARD, A. 1984. Contribution à la connaissance du développement, de l'écologie et de l'écophysiologie des Aranéides de landes armoricaines. Thèse Doct. Etat, Rennes: 389 pp., annexe: 152pp.

1987. Analyse nouvelle du développement postembryonnaire des araignées. Revue Arachnologique 7: 91-128.

CANARD, A. & STOCKMANN, R. 1992. Données comparées sur le développement postembryonnaire des arachnides. Bulletin de la Société Scientifique de Bretagne 61 n° h.s. 1, 1990: 19-50.

COINEAU, Y. 1977. La première prélarve ellatostatique connue chez les Acariens. Acarologia 19: 46-54.

CONDÉ, B. 1984. Les palpigrades: quelques aspects morpho- biologiques. Revue Arachnologique 5: 133-143.

GRANDJEAN, F. 1938. Sur l'ontogénie des Acariens. Comptes-rendus de l'Académie des Sciences, Paris 206: 146-150.

1954. Les deux sortes de temps et l'évolution. Bulletin biologique de la France et la Belgique 88: 413-433.

GUEUTAL, J. 1943. Du développement postembryon-

naire de *Phalangium opilio* L. Bulletin de la Société Zoologique de France 57: 98- 100.

GUIGUEN, C. 1990. Cycle et écologie d'*Ornithodoros (Alectorobius) maritimus* Vermeil et Marguet (Acarina: Argasidae) parasite d'Oiseaux de mer. Bulletin de la Société française de Parasitologie, Supplément 1: 316.

HENKING, H. 1882. Beiträge zur Anatomie, Entwicklungsgechichte und Biologie von *Trombidium fuliginosum* Herm. Zeitschrift für wissenschaftliche Zoologie 37: 553-663.

HOLM, A. 1940. Studien über die Entwicklung und die Entwicklungsbiologie der Spinnen. Zoologiske Biddrag Uppsala 19: 1-214.

JUBERTHIE, C. 1965. Données sur l'écologie, le développement et la reproduction des Opilions. Revue d'Ecologie et de Biologie du Sol 2:377-397.

JUDSON, M.L.I. 1990. The remarkable protonymph of *Pseudochithonius* (Chelonethi, Chthoniidae). Bulletin de la Société Européenne d'Arachnologie, n° h.s. 1: 159-165.

JUNQUA, C. 1966. Recherches biologiques et histophysiologiques sur un Solifuge saharien. Thèse Doct. Etat Paris. 124 p.

KÄSTNER, A. 1949. Zur Entwicklungsgechichte von Prosoma *Thelyphonus caudatus* L. (Pedipalpi). 2. Teil. Die Entwicklung der Mundwerkzeuge, Beinhüften und Sterna. Zoologische Jahrbücher, Anatomie und Ontogenie 70: 169-197.

LAWRENCE, R.F. 1947. Some observations on the eggs and newly hatched embryos of *Solpuga hostilis* White (Arachnida). Proceedings of the Zoological Society of London 117: 429-434.

LEGENDRE, R. 1958. Contribution à l'étude du développement embryonnaire des Araignées. Bulletin de la Société Zoologique de France 83: 60-75.

MILLOT, J. 1949. Ordre des Amblypyges. 563-588. In: P.P. Grasse (ed.). 'Traité de Zoologie'. Vol 6. Masson: Paris.

MUMA, M.H. 1966. The life cycle of *Eremobates durangonus* (Arachnida: Solpugida). Florida Entomologist 49: 233-242.

NAISSE, J. 1959. Neurosécrétion et glandes endocrines chez les Opilions. Archives de Biologie 70: 217-264.

PAVLOVSKY, E.N. 1924. Studies on the organization and development of scorpios. Quarterly Journal of Microscopical Science, London 68: 615-640.

PEREYASLAWZEWA, S. 1901. Développement embryonnaire des Phrynes. Annales des Sciences Naturelles, Zoologie. 8ème serie, 13: 117-304.

PITTARD, K. & MITCHELL, R.W. 1972. Comparative morphology of the life stages of *Cryptocellus palaezi* (Arachnida, Ricinulei). Graduate Studies Texas Tech University 1: 1-77.

POLIS, G. 1990. 'Biology of Scorpions'. (Stanford University Press: Stanford).

REUTER, E. 1909. Zur Morphologie und Ontogenie der Acariden. Acta Societatis Scientarum Fennicae 36(4): 1-288.

RUCKER, A. 1903. Further observations on *Koenenia*. Zoologische Jahrbücher, Systematik (Ökologie), Geographie und Biologie 18: 401-434.

STOCKMANN, R. 1979. Développement postembryonnaire et cycle d'intermus chez un Scorpion Buthidae: *Buthotus minax occidentalis* (Vachon et Stockmann). Bulletin du Muséum National d'Histoire Naturelle de Paris, 4ème série 1: 405- 420.

THALER, K., 1982. Die Primärlarve der Walzenspinnen *Gyllipus* cf. *cypriotica* Lawrence (Arachnida, Solifugae, Karschiidae). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 55: 93-95.

VACHON, M. 1938. Recherches anatomiques et biologiques sur la reproduction et le développement des Pseudoscorpions. Thèse Doct. Etat, Paris: 1-207; Annales des Sciences Naturelles, Zoologie, série 11: 1-207.

1940. Sur la systématique des scorpions. Mémoires du Muséum National d'Histoire Naturelle de Paris 2: 241-260.

1958a. La larve de *Galeodes arabs* C.L. K. (Arachnide, Solifuge). Comptes Rendus de l'Académie des Sciences, Paris 246: 477- 480.

1958b. Contribution à l'étude du développement post-embryonnaire des Araignées. 1è^re^ note: généralités et nomenclature des stades. Bulletin de la Société Zoologique de France 82, 1957 (1958): 337-354.

WEYGOLDT, P. 1969. 'The Biology of Pseudoscorpions'. (Harvard University Press: Cambridge, Mass.).

1970. Lebenzyklus und postembryonische Entwicklung der Geisselspinne *Tarantula marginemaculata* C.L. Koch (Chelicerata, Amblypygi) im Laboratorium. Zeitschrift für Morphologie der Tiere 67: 58-85.

1975. Untersuchungen zur Embryologie und Morphologie der Geisselspinne *Tarantula marginemaculata* C.L. Koch (Arachnida, Amblypygi, Tarantulidae). Zoomorphologie 82: 137-199.

YOSHIKURA, M. 1965. Postembryonic development of a whip scorpion, *Typopeltis stimpsonii* (Wood). Kumamoto Journal of Science, Series B Biology 7: 21-50.

1975. Comparative embryology and phylogeny of Arachnida. Kumamoto Journal of Science, Series B Biology 12: 71-142.

YSNEL, F.1992. Impact trophique et valeur bioindicatrice d'une population d'Araignées: Exemple d'une espèce à toile géométrique *Larinioides cornutus* (Araneidae). Thèse Université Rennes I. 217 pp.